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THE RELATION OF FUNGUS AND ALGA IN LICHENS.

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IF one did not constantly read, even in the newest text-books for older[1] as well as for younger students,[2] that the association between fungus and alga in lichens is uninjurious to the latter, I should not feel impelled to add to the already volumi-

[1] See *Text-book of Botany*, by Strasburger, Noll, Schenck, Schimper, translated by Porter (Macmillan Company, 1898), p. 375: The fungus derives its nourishment saprophytically from the organic matter produced by the assimilating alga, without at the same time behaving as a parasite and injuriously interfering with its vegetative activity.

In the fourth German edition (received by me, Jan. 19, 1900, as a separate) Schenck says, p. 336: Was das Verhältniss von Pilz zu Alge anbelangt, so umspinnt der Pilz mit seinem Mycel die Algenzellen, schliesst sie in ein Hyphengewebe ein und ernährt sich von den durch die assimilirenden grünen Algenzellen erzeugten organischen Stoffen; er kann aber Haustorien in die Algenzellen hinein entsenden und sogar deren Inhalt aufzehren.

[2] See Coulter's *Plant Structures* (D. Appleton & Co., 1899), p. 80: In the case of lichens the symbionts are thought by some to be mutually helpful, the alga manufacturing food for the fungus, and the fungus providing protection and water containing food materials for the alga. Others do not recognize any special benefit to the alga, and see in a lichen simply a parasitic fungus living on the products of an alga. In any event the algæ are not destroyed, but seem to thrive.

nous discussion of symbiosis in lichens. In spite of all the evidence, old and new, and in spite of common sense, the lichens are only too often described as furnishing the most perfect examples of the mutually beneficial association of two utterly different kinds of organisms, — one of these able to lead a normal and perfect existence when by itself, the other absolutely dependent for food upon other organisms, living or dead. Let me, therefore, once more direct the attention of biologists to a scrutiny of these peculiar forms.

Every one now admits that lichens consist of two distinct and separable parts, of colorless fungus-like hyphæ, which form the greater part of the mass of the lichen, and of chlorophyll-containing alga-like cells, known as gonidia. Repeatedly it has been shown that the gonidia of lichens are not merely alga-like, but are algæ, often found free in nature, growing not only on the same surfaces as furnish the seat of attachment of lichens, but on many others also, growing and multiplying as healthy individuals whenever external conditions make active life possible, passing over other periods in one or another of the resting conditions known to biologists. No one now questions that lichen gonidia are algæ, and that with due care gonidia can be identified with already known species of algæ found outside of lichen associations. Identification on mere inspection of the gonidia in the lichen is not always possible, nor would it always be correct. For example, Hedlund[1] says that the alga which forms the gonidia in species of Micaria usually looks like Glœocapsa and frequently occurs on rotten wood, but that, when cultivated on this wood under abundant illumination and free from fungus enemies or algal competitors, the alga multiplies rapidly, becomes deep green, the daughter-cells separate, and none has the thick gelatinized wall which is one of the characters of Glœocapsa. Conditions wholly external to the algal cells, especially such influences as affect their freedom, cause these cells to depart from their Protococcus type and to develop qualities and habits characteristic of a wholly

[1] Hedlund, T. Kritische Bemerkungen über einige Arten der Flechtengattungen Lecanora, Lecidea, und Micarea. *Bihang till K. Svenska Vet. Akad. Handlingar*, Bd. xviii. Stockholm, 1892.

different genus. Assuming that Hedlund's experiments were conducted with sufficient cleanliness to prevent Protococcus from replacing Glœocapsa, this return from Glœocapsa-like characters to the original Protococcus characters is interesting evidence of the influence of living competitors (other algæ) and enemies (fungi), as well as of lifeless forces (light, food, etc.), upon the appearance of living organisms. Since small algæ are so modified, both inside and outside of the lichen body, by external influences, their identification and the identification of gonidia become in some instances matters of difficulty, in which experiment must play an important part.

As to the fungus-like component of lichens, all are now agreed that the hyphæ are fungus, but the identity of any fungus component of lichens with species of fungi living otherwise is difficult to prove and is absolutely denied by many. According to Reinke,[1] the fungus components of the lichens of to-day came from fungi no longer existing as distinct species. That this is necessarily true it is impossible to see; that it is true is hard to believe, for, as has been shown above for the gonidia, the other organisms with which it is associated, as well as the lifeless forces to which it is subjected, may so influence an organism that its appearance and behavior will be profoundly modified. Although Möller's[2] now classical experiments in cultivating the fungus components of certain simple lichens on artificial media were successful as far as they went, they did not go so far as to show that the fungus could reproduce itself by ascospores formed in normal apothecia, and, after all, only lichens of simple thallus form were cultivated at all. It is only natural, but also greatly to be regretted, that the extremely slow growth of lichens and of their fungus components has deterred most botanists from experimenting on these interesting plants. Reinke's view can be proved or disproved only by successful culture of

[1] Reinke, J. Abhandlungen über Flechten, III. *Jahrb. f. Wiss. Bot.*, Bd. xxviii (1895), p. 64: Kein Flechtenpilz ist bisher im freilebenden Zustande beobachtet worden — abgesehen von den Basidiolichenen — und es hat demnach den Anschein, dass alle Pilze, aus denen sich Flechten entwickelt haben, als Pilze zu Grunde gegangen sind.

[2] Möller, A. Ueber die Cultur flechtenbildender Ascomyceter ohne Algen. *Inaug. Diss.* Münster, 1887.

the fungus from spore to spore, and whether or not we believe with him that the fungus components of lichens no longer exist by themselves in nature, we certainly must call them fungi.

What is a fungus? However a systematist might answer this question, a physiologist would say that a fungus is a low dependent plant, demanding at least non-nitrogenous food in a state of comparatively high elaboration (sugar, fat, oil, or similar carbon compounds), since it is unable to manufacture such food for itself. It follows, therefore, that a fungus must be either parasitic or saprophytic, or, to follow the newer terminology,[1] metatrophic or paratrophic. When a fungus enters into association with an alga to form a lichen, the fungus allies itself with an independent plant, one able to manufacture all of its own food. The lichen is then composed of a dependent plant which must receive elaborated food, and of an independent plant which needs only food materials and light in order to take care of itself. What then is the nature of the association between these two? Reinke[2] and his sympathizers believe (*a*) that the association is consortism; (*b*) that the two members of the consortium are dependent upon and beneficial to each other; and (*c*) that the consortium is autonomous. On the other hand, many botanists, probably in the minority at the present moment, see in this association not a mutually advantageous association, but the parasitism of one plant upon another. Reinke,[3] de Bary,[4] and many others assert that the association of fungus with alga in lichens cannot be simple parasitism because, if this were the case, the fungus would consume the alga, and that would be the end of the association. Such a conclusion is not required by the evidence. It must first be shown that the influence of the fungus is so violent and so exhausting that the alga is not able, by producing slightly more food, by refraining from less economical ways of repro-

[1] Fischer, A. Vorlesungen über Bakterien, pp. 47, 48. Jena, 1897.

[2] Reinke, J. Abhandlungen über Flechten. II. Die Stellung der Flechten im Pflanzensystem. *Jahrb. f. Wiss. Bot.*, Bd. xxvi, pp. 524–542, 1894.

[3] Reinke, J. *Loc. cit.*, Bd. xxvi, p. 530, etc.

[4] de Bary, A. Die Erscheinung der Symbiose. Strassburg, 1879.

duction (*e.g.*, zoöspore formation), by dividing in certain planes instead of in others, etc., to meet the extra demand made upon it by the fungus and to form some cells which are affected only indirectly, if at all, by the fungus.[1]

On these points a few remarks may be made. In the first place, those algæ which form the gonidia of lichens will grow and multiply faster under almost any conditions than the fungus, and they grow and multiply in lichens less rapidly than under favorable conditions outside. In the lichen itself they grow and multiply very rapidly at times, much more rapidly than the fungus. For example, the gonidia in a fragment of *Ramalina reticulata*, the California lace-lichen, may be made to grow and to divide very rapidly by placing the piece in water in the comparative warmth of the laboratory in winter. The whole lichen does not grow; only the gonidia multiply and grow; the fungus grows but little, if at all. Out of doors such conditions frequently occur in all lichens. During warm rains or fogs, or dews, the gonidia have the advantage; they multiply and grow much more rapidly than the fungus; many gonidial cells recover what they had lost by too intimate association with the fungus. In this way new generations of gonidial cells are produced which continue the race in the lichen body and thereby prevent the fungus from devouring all at once. In other words, though the fungus may be parasitic upon the alga, the more vigorous alga is not wholly and at once consumed by its parasite, whatever may be the ultimate fate of the gonidial cells one by one.

Having seen that the association of fungus and alga in lichens is not destructive to all the algal cells at once, it must be shown whether the fungus is destructive or injurious to any. In all lichens the hyphæ and gonidia are in most intimate contact, the hyphæ either closely clasping the gonidial cells or filaments, or actually sending one or more haustoria into the separate gonidial cells. As a result of such intimate contact, osmotic movement of food and other substances must take

[1] Hedlund, T. *Loc. cit.* Peirce, G. J. The Nature of the Association of Alga and Fungus in Lichens. *Proc. Cal. Acad. Sci.*, Third Series, Botany, vol. i, No. 7, 1899.

place between the hyphæ and the invested gonidia. That such a movement does not take place it is impossible to believe unless one assume that the nature of the limiting membranes of algal and fungal cells is such that osmosis is a physical impossibility. This assumption would be self-destructive, however, for if these membranes were impervious to the dissolved substances in the algal and fungal cells, all osmosis would be impossible, and the cells would all die from lack of food and water. There must then be osmotic movement between fungus and alga. In obedience to the ordinary laws of osmosis there would be movement of dissolved substances from regions of more to regions containing fewer molecules of these substances. The alga under the influence of light manufactures complex nutritious non-nitrogenous carbon compounds, which are at times, if not always, in soluble forms. These substances would tend to migrate from the algal to the fungal cells. This physical phenomenon is of the utmost physiological importance to the fungus, for it thereby gains the food it needs. Such a transfer is inevitable so long as the conditions of intimate contact, of permeable membranes, of supply of food and demand for it continue the same. If the demand for food by the fungus or any part of it exceed the ability of the alga, or of any algal cell, to manufacture enough for its own needs and those of the fungus, the fungus will consume the alga itself. The numbers of empty gonidial cells in the lichen body are sufficient evidence of this,[1] but this evidence cannot always be found, for only at times does the fungus demand so much of the alga that the body substance of the alga must be given to feed the fungus.

The slow-growing fungus component of the lichen draws food from the more rapidly growing algal cells in which the food is manufactured. Such taking of food is evidently parasitism. It can be nothing else. The intimacy of contact of hyphæ and gonidia precludes any other supposition than that the hyphæ osmotically draw food from the necessary and helpless algæ. If the algæ grew and multiplied less rapidly, or if the fungus grew more rapidly, or if the alga made less and the fungus demanded more food, or even if fungus and alga always

[1] Peirce, G. J. *Loc. cit.*, p. 225, etc.

grew at a constant rate instead of the alga sometimes growing much faster than the fungus, the parasitism of fungus on alga would result much sooner in the destruction of each algal cell. As it is, the fungus destroys the algæ, but only by degrees, and so slowly that a new generation is mature before the first is consumed.

If there is osmotic transfer of non-nitrogenous food from alga to fungus, there may also be osmotic transfer of something else from fungus to alga. Presumably there is. De Bary, Reinke, and others say that the fungus supplies the alga with water and mineral salts. Undoubtedly this is true, but I doubt this being other than by the capillary movement of columns or films of water, holding mineral salts in solution, between and along the hyphæ which, running more or less parallel with one another, form continuous capillary tubes from the substratum throughout the body of the lichen. By this means the fungus certainly does supply the alga, but so would cotton fibres or glass tubes similarly placed. It cannot be questioned that, in its position in the lichen, the alga needs to have water and mineral salts conducted to it, but its position is not of its own seeking, natural, or necessary, or at all evidently advantageous. In its natural habitat the alga (Protococcus, Glœocapsa, Nostoc, etc.) could supply itself with aqueous solutions of needed food materials without thê intervention of a dearly paid servant.

It is alleged by some that what the fungus obtains from the alga is merely the excess of organic matter elaborated by the latter, and that the alga is manured by the waste substances produced by the fungus. Such conceptions of the physiology of living organisms are anything but definite. According to this, plant cells and plant bodies are leaky affairs from which nutritious substances ooze in appreciable quantities. Every one knows that this is not true. The ooze theory of the nutrition of the associates in the lichen must, therefore, be abandoned.

It is said that, if the fungus were simply parasitic upon the alga, the algal cells would not so rapidly multiply, would not look so healthy as they often do in the lichen thallus. Besides the reason already given for this, it seems to me certain, from my study of *Ramalina reticulata*, and of some others

of our California lichens,[1] that the algal cells invested or penetrated by fungus filaments try by frequent division to produce cells which shall be quite free from contact with hyphæ. The contact of the hypha exerts an irritation which induces more frequent division, and at a smaller size than normally takes place in gonidia not in contact with hyphæ. Gonidia may frequently be found in the lichen thallus, large and wholly free from contact with hyphæ. These gonidia divide less frequently than the others and are by all means nearest the typical algal cells of the same species in size, color, form, thickness, and composition of wall, etc. These free gonidia are fed with water and mineral salts, are protected against drought and certain other dangers, and may really benefit by being enclosed in a mass of fungus hyphæ. Gonidia which are not merely loosely enclosed in the lichen body but are tightly invested if not penetrated by hyphæ, although they may be supplied with food materials and may be protected, are also robbed of part of the food they elaborate and are actually irritated by their associate. That they are ultimately sucked dry by the fungus I have recently shown in the paper already referred to.

In an increasing number of lichens it is being found that the hyphæ not merely closely invest the gonidia, thereby making possible the osmotic movement of elaborated food from alga to fungus, but that the hyphæ actually penetrate the gonidia by haustoria. These haustoria either apparently merely penetrate the cell-wall, pushing back the protoplasm, or they actually penetrate the protoplasm also. Where it is possible to demonstrate in any species of lichen that haustoria actually occur in the gonidia, there can be no doubt that the association is of unmixed injury to the alga, and of unmixed benefit to the fungus. The movement of aqueous solutions through the haustoria from the gonidia to the hyphæ is different, however, only slightly in degree and not at all in kind from that which takes place between gonidia and closely clasping hyphal branches. The absorption of food is easier, the parasitism more perfect and more evident, when haustoria connect hyphæ and gonidia

[1] Peirce, G. J. *Loc. cit.*

than when the hyphæ merely enclose the gonidia, but the hyphæ are parasitic in both cases.

The foregoing argument, based on observations reported in detail elsewhere,[1] shows, I believe, that there are no physiological or structural reasons for supposing that the association of fungus and alga in lichens is other than the actual parasitism of the former upon the latter. If the lichens are merely fungi and algæ associated together as parasite and host, these associations are no less remarkable and interesting, though less moral, than if they were ideal alliances for mutual aid. Experiment has still to show whether the characters of the lichen thallus are formed by the fungus mainly, or by the fungus under the influence of its host, how far substratum, illumination, nutrition, etc., affect the character of the association. Experimentation on lichens demands endless patience and considerable skill, for lichens grow with prodigious slowness, and the chances of a culture becoming infested with mould or bacteria before it has accomplished the purpose designed are only too great. Some of the problems puzzling systematic lichenologists can be solved only when illuminated by experimental culture of the fungus component of the lichen thallus under definitely known conditions.

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[1] Peirce, G. J. *Loc. cit.*